

ANNUAL RETURN RATES OF BREEDING GRASSLAND SONGBIRDS

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ABSTRACT.—We used reobservation of color-banded birds to index annual breeding site fidelity of four species of songbirds that nest in the northern mixed-grass prairie of northcentral Montana (1996–2005). Territorial males of Sprague’s Pipits (*Anthus spragueii*), and Savannah (*Passerculus sandwichensis*), Grasshopper (*Ammodramus savaunarium*), and Baird’s (*A. bairdii*) sparrows were located on five permanent study sites (1998–2004) and lured into mist-nets using tape broadcasts of conspecific songs and calls. The proportion reobserved was 5.3% ($n = 247$) across all banded adult males. Grasshopper Sparrows had the highest proportion of returns (8.9%), followed by Savannah Sparrows (5.4%), Baird’s Sparrows (5.1%), and Sprague’s Pipits (2.1%). Three nestling Savannah Sparrows were reobserved in subsequent years ($n = 193$), while no nestlings of the other species were reobserved ($n = 401$). Our return rates were low for all adults in comparison with typical reports of return rates for songbird species of woodland and shrubland habitats. Migratory nomadism may explain this phenomenon, where grassland migrants are opportunistic in site selection, rather than faithfully returning to potentially uninhabitable former breeding sites. Received 20 December 2005. Accepted 9 August 2006.

Breeding site-fidelity is defined as the tendency of a migratory bird to return to a previous breeding site. Numerous studies have documented strong breeding site-fidelity in some migratory birds (Gavin and Bollinger 1988, Green 1992, Murphy 1996, Porneluzi 2003), especially for those species that nest in shrubland and forested habitats (Porneluzi and Faaborg 1999, Gardali et al. 2000). The return of migratory birds to earlier breeding sites demonstrates remarkable orientation and suggests strong evolutionary benefits to returning to the same area to breed, particularly when successful breeding has occurred at a site in the past (Gavin and Bollinger 1988, Porneluzi 2003). However, the potential benefits of returning to previously successful breeding sites could be negated if nesting habitat is highly variable from year-to-year, possibly becoming unsuitable in some years.

Grasslands of the northern prairies are dy-

amic environments with fluctuating conditions that, depending on scale and feature, are unpredictable in time and space, creating a mosaic of habitat conditions (Ahlering 2005, Winter et al. 2005). This variability is due to many causes, including effects of lightning- and human-set fires (Higgins 1984), intense grazing by prairie dogs (*Cynomys* spp.), bison (*Bison bison*), and other ungulates (Kirsch and Kruse 1973) and, perhaps most importantly, widely fluctuating precipitation levels across years (Igl and Johnson 1999, Ahlering 2005). Alternating periods of drought and above-average precipitation result in fluctuations in the structure and floristics of grasslands, within and between years (Winter et al. 2005). Strong annual variation in breeding habitat conditions can cause tremendous shifts in local and regional bird population densities (Fretwell 1986, Igl and Johnson 1999, Winter et al. 2005). Evidence suggests that some grassland birds have adapted to this variability by exhibiting low site fidelity, often resulting in spectacular fluctuations in local population densities (Cody 1985, Igl and Johnson 1999, Winter et al. 2005). Many grassland bird species have evolved nomadic strategies for breeding site selection since habitat instability makes it potentially unprofitable, even for previously successful nesters, to return consistently to the same grassland breeding areas

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(Andersson 1980). Nomadism is defined as the tendency of adults and juveniles to move widely in response to resources that are patchy in time and space (Andersson 1980, Johnson and Grier 1988). Nomadic behavior is a selectively advantageous alternative to site-fidelity for grassland birds (Cody 1985), and is indicated by relatively low return rates, when compared with return rates of birds inhabiting more stable environments (e.g., shrublands and forests).

Site fidelity studies of grassland bird populations are largely restricted to eastern North America. Sedge Wrens (*Cistothorus platensis*, Herkert et al. 2001), Henslow's (*Ammodramus henslowii*, Herkert et al. 2002), Le Conte's (*A. leconteii*, Murray 1969), and Nelson's Sharp-tailed (*A. nelsoni*, Murray 1969) sparrows all had return rates that were lower ($\leq 13.5\%$) than those typically reported for woodland and shrubland nesting passerines. However, Bobolinks (*Dolichonyx oryzivorus*), whose return rates varied from 44 ($n = 85$) to 70% ($n = 79$) for adult males (Gavin and Bollinger 1988, Bollinger and Gavin 1989, Martin and Gavin 1995), have return rates that are more commensurate with shrub and forest dwelling species (Green 1992). Dickcissel (*Spiza americana*) also showed a tendency to return to former breeding sites in the center of their range (Fretwell 1986), with a return rate of 49% ($n = 82$) in Kansas (Temple 2002).

We investigated breeding songbird site fidelity in the mixed-grass prairie of northcentral Montana. Four co-occurring species were studied: Sprague's Pipits (*Anthus spragueii*), and Savannah (*Passerculus sandwichensis*), Grasshopper (*Ammodramus savannarum*), and Baird's (*A. bairdii*) sparrows. Data on grassland birds in the northern Great Plains are relatively scarce; no other return rate studies have been published on Sprague's Pipits with only one study on Baird's Sparrows (Green 1992).

METHODS

Study Area.—Our study was conducted at Bowdoin National Wildlife Refuge (NWR) in Phillips County, northcentral Montana (48° 24' N, 107° 39' W; ~750 m elevation). Data were collected during summers of 1996–2004 on five permanently located sites (26–59 ha)

1.3–10.1 km apart, comprising 218 ha of flat to gently rolling native mixed-grass prairie. Blue grama (*Bouteloua gracilis*), needle-and-thread (*Stipa comata*), western wheatgrass (*Pascopyrum smithii*), and dense clubmoss (*Selaginella densa*) were the dominant herbaceous species. Shrubs were sparse and trees absent. Bowdoin NWR has not been grazed by cattle for ≥ 29 years. One study site was partially burned in 1994 and one site was prescribed burned in 2000; otherwise, no burning events have occurred since refuge documentation began in 1936.

Capture and Marking.—Known territorial adult males were lured into 30- or 36-mm mesh mist nets using tape playback recordings of conspecific song beginning in 1998 (Sogge et al. 2001). We used Sony TC-D5Pro II or Marantz PDM 430 cassette recorders amplified by an AmpliVox s805 Multimedia Amplifier, connected into two tweeters by 30–50 m of 16-gauge speaker cord. Speakers were placed on either side of a 12-m mist net within the territory of a target male. Tape playback of conspecific song was broadcast to draw the target male into the net. Carved wooden decoys were placed at the net as visual lures beginning in 2003.

Each individual captured was marked with a uniquely numbered federal aluminum band, plus three color bands whose colors were randomly selected. Sprague's Pipits were banded with a year cohort color band, and a color band denoting gender and age. Incidental females captured at the net were also banded. Nestlings were banded, beginning in 1996, with a year cohort color; processing occurred on day 7 or 8 post-hatch (Dieni and Jones [2003] describe nest searching methods). Gender for adults was assigned based on the presence of a cloacal protuberance for males or brood patch for females; gender of hatching-year birds could not be assigned.

Returns.—Field assistants identified the banding status of all observed individuals among target species during nest searching activities from May to August 1997–2005. All individuals of the target species were checked for bands either by capture of territorial males or visually using binoculars and spotting scopes on all study sites. In addition, the target species were also visually observed, or oc-

TABLE 1. Grassland bird banding at Bowdoin National Wildlife Refuge, Montana. Adult male banding effort from 1998 to 2004, nestlings (gender unknown) 1996–2004, returns 1997–2005.

Species	No. banded		No. returned		%	
	Adults	Nestlings	Adults	Nestlings	Adults	Nestlings
Sprague's Pipit	48	160	1	0	2.1	0.0
Savannah Sparrow	37	193	2	3	5.4	1.6
Grasshopper Sparrow	45	138	4	0	8.9	0.0
Baird's Sparrow	117	103	6	0	5.1	0.0
Totals	247	594	13	3	5.3	0.5

asionally captured off-site throughout Bowdoin NWR.

Male Sprague's Pipits were generally detected only during territorial displays that occurred 50–100 m above the ground (Robbins 1998). Thus, reobservation required either recapture or luring individual males within viewing distance using tape playback of conspecific song. We also were able to reobserve individual Sprague's Pipits in nests monitored with miniature video cameras (SLJ and PJG, unpubl. data).

We assumed no significant effect of capture, handling, or bands on return rates; to our knowledge, there were no capture-related injuries or mortality. Similar techniques did not negatively affect return rates of female Wood Thrushes (*Hylocichla mustelina*), including hatching-year birds (Perkins et al. 2004). Analysis of the use of colored bands (most of the same colors that were used here) on a migratory population of American Goldfinches (*Carduelis tristis*) showed that color bands did not appear to affect return rates (Watt 2001).

RESULTS

Return Rates.—Thirteen banded adult males were reobserved (5.3%, $n = 247$) (Table 1). Grasshopper Sparrows had the highest proportion of adult male returns (8.9%), followed by Savannah Sparrows (5.4%), Baird's Sparrows (5.1%), and Sprague's Pipits (2.1%) (Table 1). Ten of the 13 reobserved adult males were confirmed to have returned to the same site where they were originally captured. The remaining three (one each for Sprague's Pipit, and Grasshopper and Baird's sparrows) could not be identified to individual and we were unable to identify their sites of origin.

Capture Effort.—Our targeted mist-netting

technique was effective in capturing territorial adult males of all target species. Using the number of nests located as an index to territory abundance, our capture ratio of adult males to number of known nests was less than one for Savannah Sparrows (0.24), Sprague's Pipits (0.62), and Grasshopper Sparrows (0.63). However, our capture ratio exceeded unity for Baird's Sparrows (2.6), which suggests that our sample may have included transients, as well as individuals whose nesting attempts had failed earlier in the season.

We banded Savannah Sparrow nestlings ($n = 193$) of which 1.6% were reobserved in subsequent years; no banded nestlings were re-sighted among the other target species ($n = 401$) (Table 1). Two of the reobserved Savannah Sparrow nestlings were identified to individual; one was observed at its natal site, and one was reobserved 4.8 km from its natal site. Ten female Savannah Sparrows were captured incidentally at the net. Among these, one adult female returned two consecutive years post-capture to the same site.

DISCUSSION

Three patterns of breeding-ground settling have been described for upland grassland waterfowl, characterized as homing, opportunistic, and flexible (Johnson and Grier 1988). Homing, where adults return to the same breeding area used before, is thought to be a response to relatively stable and ostensibly more predictable habitats. Opportunistic settling, where the individual settles in the first suitable site encountered in its breeding range, regardless of conditions in former breeding areas, is generally thought to be a response to less stable (less predictable) habitats. Flexible settling is where the individual will return to an area used previously, but moves elsewhere

if that area has become unsuitable. Opportunistic or flexible settling would be expected to occur more frequently in endemic grassland birds than homing as an evolutionary response to habitat variability inherent in grasslands. Indeed, many grassland bird populations undergo considerable annual changes in distribution and abundance in the northern Great Plains (Johnson and Grier 1988, Shane 2000, Herkert et al. 2001, Green et al. 2002).

Annual return rates for all species reported here suggest low site fidelity. Reviews of studies of woodland and shrubland migratory passerines reported a mean return rate of ~ 46% for adults (Green 1992, Johnson and Geupel 1996, Gardali et al. 2000). Our study is consistent with a return rate of 5.3% ($n = 95$) reported for Baird's Sparrows in North Dakota (Green 1992). Moreover, it has been suggested that lack of geographic variation in bird songs (e.g., Baird's Sparrows) may also indicate an opportunistic settling pattern, since regional dialects would have difficulty forming in populations with substantial between year mixing (Kroodsmas and Verner 1978, Green 1992, Kroodsmas et al. 1999).

Our data are inconsistent with some reobservation data for Savannah and Grasshopper sparrows from other geographic regions of their respective breeding ranges (Bedard and LaPointe 1984, Wheelwright and Rising 1993, Vickery 1996). Multiple studies of Savannah Sparrows in eastern North America showed a mean return rate of 46.1% (SLJ, unpubl. data), primarily in grasslands but including salt marsh (Bedard and LaPointe 1984). Nestling Savannah Sparrows showed natal philopatry in New Brunswick island habitats (Wheelwright and Rising 1993). Grasshopper Sparrow return rates varied geographically, being lower in the Midwest and prairie regions than in the East, with return rates varying between 0 and 52% for migratory populations (Kaspari and O'Leary 1988; Vickery 1996; Balent and Normont 2003; B. K. Sandercock, pers. comm.). In Connecticut, 50% ($n = 10$) of those banded in 1986 returned in 1987; in Kennebunk, Maine, male return rate was estimated at 35% ($n = 42$) during a 3-year period; in California, 20% ($n = 35$) of the adult males returned (Vickery 1996). Return rates for Grasshopper Sparrows in the Midwest were lower with 19.8% ($n = 111$) adult males

returning to Fort Riley in Kansas (B. K. Sandercock, pers. comm.), while no banded adults or juveniles ($n = 85$) were reobserved during a five-year study on Arapaho Prairie, a mixed-grass prairie in the Sandhills of Nebraska (Kaspari and O'Leary 1988).

Our relatively low reobservation rates suggest three possibilities: (1) low probability of reobservation of banded individuals, (2) low survivorship, and (3) low site-fidelity. Reobservation of adults on-site was straightforward and not problematic, although only limited time was spent searching adjoining areas for banded individuals. We were unable to calculate meaningful survivorship estimates using mark-recapture statistics since our return rates were too low (Murphy 1996). Therefore, either our survival was much lower than rates typically estimated for passerines, which seems unlikely, or our return rates were actually low and many of the adults that did not return moved to new breeding sites. Discounting low reobservation and survivorship, our results indicate a nomadic migratory pattern for our study species, suggesting opportunistic or flexible settling patterns, indicative of species adapted to historically unstable breeding habitats (Owens and Myers 1973, Andersson 1980, Johnson and Grier 1988). However, we cannot ignore the fact that some of our birds returned to our sites to breed; indeed, Green (1992) also found that a small number of Baird's Sparrows returned and bred in the same territories in subsequent years. This suggests that at least a small percentage of individuals of these species are site faithful while the rest settle with flexible or opportunistic patterns.

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